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# STUDIES IN NEOTROPICAL PALEOBOTANY. X. THE PLIOCENE COMMUNITIES OF PANAMA—COMPOSITION, NUMERICAL REPRESENTATIONS, AND PALEOCOMMUNITY PALEOENVIRONMENTAL RECONSTRUCTIONS<sup>1</sup>

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Alan Graham<sup>2</sup>

## ABSTRACT

The middle Pliocene Gatun Formation of central Panama consists of carbonaceous sandstones and siltstones preserving a pollen and spore flora of 110 recognized types. The most abundant are *Operculodinium* and *Spiniferites* (dinoflagellates), *Alsophila*, *Pteris*, monolet fern spores, Gramineae, Palmae, *Casimiroa*, *Combretum/Terminalia*, *Eugenia/Myrcia*, *Faramea*, *Ilex*, Malpighiaceae, and *Rhizophora*. These sort into 11 principal paleocommunities: shallow water marine community, mangrove swamp, floating/submerged fresh water aquatic community, lowland fresh water marsh community and fringing vegetation, and tropical wet, tropical moist, premontane wet, premontane moist, premontane rain, lower montane moist, and tropical dry forests. The primary differences between the middle Pliocene Gatun communities and older Eocene and lower Miocene vegetation are (1) increased biotic diversity, (2) the first appearance of substantial quantities of grass pollen (maximum 7.5%), (3) a more fully developed and extensive tropical dry forest, (4) increased physiographic diversity, (5) better representation of lower montane forests, and (6) possibly, the first indication of developing wetter Atlantic and drier Pacific provinces in southern Central America.

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An assemblage of 110 fossil pollen and spores, including 13 with no previously known fossil record and 27 unknowns, has been recovered from the middle Pliocene Gatun Formation of central Panama. The systematics of the Gatun flora has been presented earlier (Graham, 1990, 1991a, b), and the geology is summarized in Graham et al. (1985). This paper concludes the study with presentation of the composition, numerical representations, and paleocommunity/paleoenvironmental reconstructions.

## MATERIALS AND METHODS

Extraction, slide preparation, and photographic techniques are discussed in Graham (1985). Terminology for vegetation types follows Holdridge (1947; Holdridge et al., 1971), and distributions and community assignments are based on Croat (1978) and D'Arcy (1987). Depths along the core are given in feet, following the original log data.

## COMPOSITION AND NUMERICAL REPRESENTATIONS

The composition, distribution, and percentage for each palynomorph at the nine levels along the Gatun core are given in Table 1. The distribution of the 15 most abundant microfossils (2% or greater from at least one level) is presented in Figure 1.

Sediments in the lower portions of the profile (257.0–253.0') consist of fine- to medium-grained sandstone with interspersed lenses of coalified lignite. The sandstone suggests near-shore deposition as rivers and surface waters slow and drop heavier mineral particles first upon entering the ocean. The environmental setting was paralic (marine coastal), tropical to warm-temperate (presence of *Rhizophora*), estuarine (bay), and low-energy where autochthonous organic material accumulates rather than being dispersed by coastal currents. Percentages of *Rhizophora* pollen are relatively low (3.0%, 2.5%, 5.0%; Fig. 1). The lower portion of the core

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<sup>2</sup> Department of Biological Sciences, Kent State University, Kent, Ohio 44242, U.S.A.



TABLE 1. Identification and numerical representation of fossil palynomorphs from the Gatun Formation, Panama. Percentages are based on counts of 200 from slide 1 of each sample. (—) indicates specimen not encountered in tabulation.

Species	Depth (feet)								
	257.0	255.5	253.0	250.0	223.5	223.0	222.5	178.0	162.0
Pyrrophyta	—	—	—	—	7.5	7.0	7.5	—	—
Lycopodiaceae									
<i>Lycopodium</i>									
type 1	—	—	—	—	1.0	—	—	—	—
type 2	—	—	—	—	—	—	—	—	—
type 3	—	—	—	—	1.5	—	—	—	—
type 4	—	—	—	0.5	—	—	—	—	—
Selaginellaceae									
<i>Selaginella</i>	—	—	—	—	1.5	—	—	—	—
Cyatheaceae									
<i>Alsophila</i>	3.5	—	3.5	—	6.0	8.0	8.0	3.0	9.0
<i>Cnemidaria</i>	1.5	—	0.5	—	—	—	—	1.5	—
<i>Cyathea</i>									
type 1	—	—	1.5	—	1.5	1.5	—	1.5	1.5
type 2	—	—	—	—	—	—	—	—	—
Ophioglossaceae									
<i>Ophioglossum</i>	—	—	—	—	—	—	—	—	—
Polypodiaceae									
<i>Grammitis</i>	—	—	—	—	1.0	—	—	—	—
Pteridaceae									
<i>Ceratopteris</i>	—	—	—	—	1.0	1.5	—	1.5	1.5
<i>Pteris</i>									
type 1	—	—	—	—	—	—	—	—	—
type 2	—	—	—	—	—	—	—	—	—
type 3	—	—	—	—	—	—	—	—	—
type 4	—	—	—	0.5	3.5	7.0	8.5	8.5	10.0
type 5	—	—	—	—	—	—	—	—	—
Trilete fern spore									
type 1	0.5	0.5	—	—	—	—	—	—	—
type 2	—	—	—	—	—	—	—	—	—
Dryopteridaceae									
<i>Ctenitis</i>									
type 1	1.5	0.5	1.0	—	—	1.0	—	1.5	—
type 2	—	—	—	—	—	—	—	—	—
type 3	—	—	—	—	—	—	—	—	—
Monolete fern spore									
type 1	14.0	8.5	8.0	1.5	9.0	14.0	13.0	14.0	26.0
type 2	7.0	13.5	9.5	3.0	11.5	8.5	4.5	24.0	16.0
type 3	—	—	—	—	—	—	—	—	1.0
type 4	—	—	—	—	—	—	—	—	—
type 5	—	—	—	—	—	—	—	—	—
Podocarpaceae									
<i>Podocarpus</i>	1.0	1.0	—	—	—	—	—	—	—
Gramineae	7.5	6.5	4.5	—	—	1.0	—	—	—











TABLE 1. Continued.

Species	Depth (feet)								
	257.0	255.5	253.0	250.0	223.5	223.0	222.5	178.0	162.0
Unknown									
1	—	0.5	3.5	—	—	1.5	—	1.0	—
2	—	—	2.5	—	—	—	—	—	—
3	—	—	—	—	—	—	—	—	—
4	2.5	5.0	1.5	—	—	—	—	—	—
5	—	—	—	—	—	—	—	—	—
6	1.5	—	—	—	2.0	—	—	—	—
7	1.5	—	3.0	—	—	0.5	—	—	—
8	—	0.5	—	—	—	—	—	—	—
9	—	—	—	—	—	—	—	—	—
10	—	—	—	—	—	—	—	—	—
11	—	—	—	—	—	—	—	—	—
12	—	0.5	—	—	—	—	—	—	—
13	—	—	—	—	1.0	—	—	—	—
14	—	—	2.5	—	—	—	—	—	—
15	—	0.5	—	—	—	—	—	—	—
16	—	0.5	—	—	—	—	—	—	—
17	—	—	—	0.5	—	—	2.0	—	—
18	—	—	0.5	—	—	—	—	—	—
19	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—
21	—	—	—	—	—	0.5	—	—	—
22	—	—	0.5	—	1.0	0.5	—	—	—
23	—	—	—	—	—	—	—	—	—
24	—	0.5	2.5	—	5.0	4.5	3.5	—	4.0
25	—	—	3.0	—	—	—	—	—	—
26	—	—	3.0	—	—	—	—	—	—
27	2.0	1.5	2.0	0.5	1.5	—	—	1.0	—
Other unknowns	12.5	9.0	10.0	0.5	12.0	10.5	9.0	8.0	10.5

is characterized by high percentages of monolete fern spores (combined values 21%, 22%, 17.5%) and palm pollen (19.5%, 32%; Table 1), and relatively high percentages of grass pollen (7.5%, 6.5%, 4.5%). The figures for grass pollen are significant when compared to values for older floras from the same region. Maximum percentages for grass pollen in the middle(?) to upper Eocene Gatuncillo and the lower Miocene Culebra, Cucaracha, and La Boca floras of central Panama, and the Uscari sequence flora of Costa Rica (Graham, 1985, 1988a, b, 1989a, 1987a) are 0%, 1%, 0%, less than 1%, and 0%, respectively. The appearance of comparatively large amounts of grass pollen in the middle Pliocene Gatun flora is one of the principal differences between it and older Tertiary floras from the same region.

At level 250' a major change in microfossil percentages occurs, with *Rhizophora* pollen reaching 82% of the total flora. This compares to previous values of 3.0%, 2.5%, and 5% at levels

257.0, 255.5, and 253.0', respectively (Table 1, Fig. 1). All other major pollen and spore types decrease in value (Fig. 1), or disappear completely. Only 16 palynomorph types (14%) were encountered at level 250', compared to 48 types (44%) for the preceding three levels. Monolete fern spores decrease from combined values of 21%, 22%, and 17.5% to 4.5%, and palm pollen decrease from 19.5%, 32%, and 10.5% in the three lowest levels to 4.5% at level 250.0'.

A change in sediment type, and in the microfossil assemblage, occurs at levels 223.5–222.5'. The sediment particle size changes from a fine- to medium-grained sandstone with lenses of lignite, to a finer siltstone with organic matter dispersed through the sediment. Smaller-grained particles remain suspended longer upon entering the ocean and are characteristic of sedimentation further from the shore where currents disperse the microscopic-size organic component. The principal change in the microfossil flora at levels 223.5–222.5' is the first



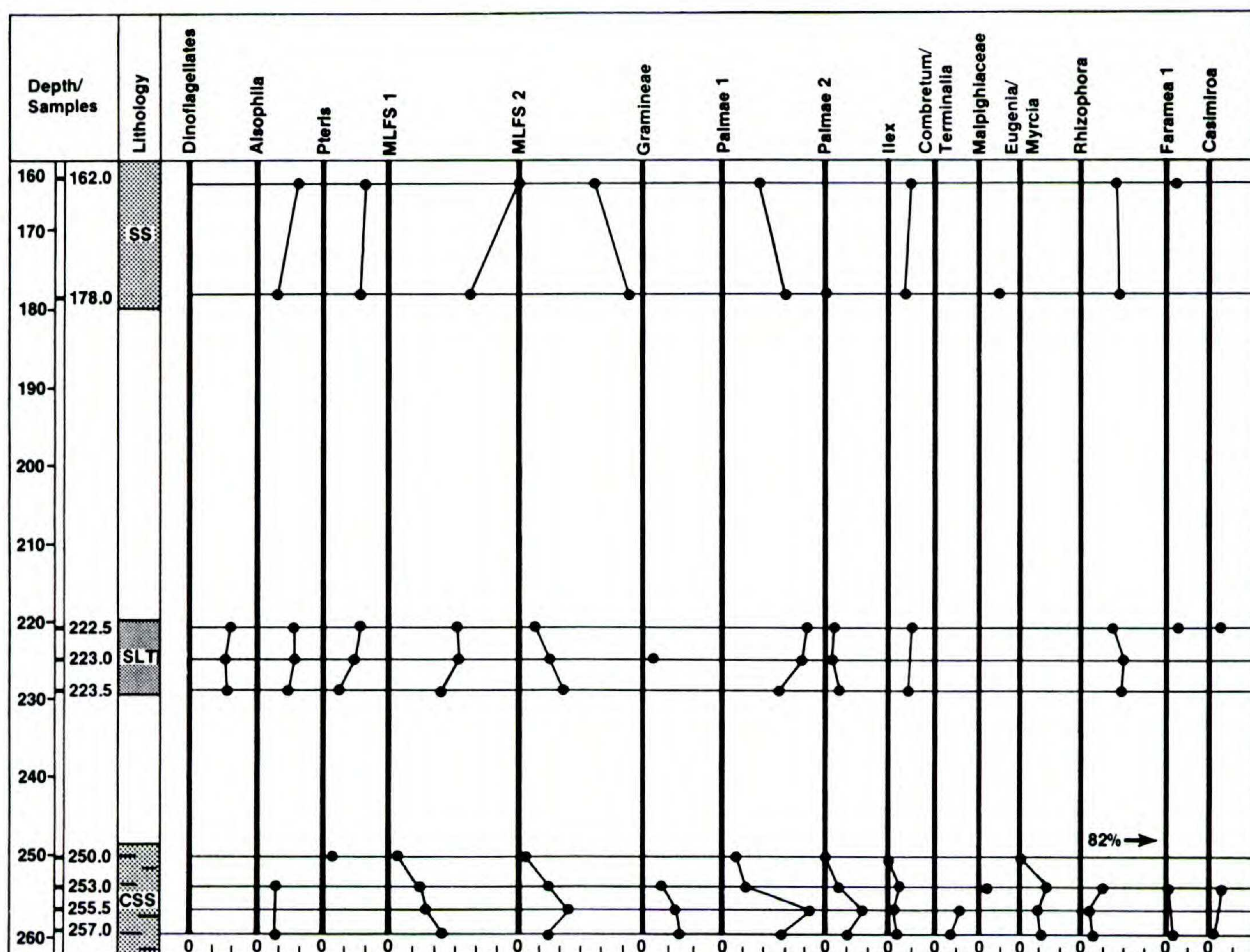


FIGURE 1. Vertical distribution of the most common palynomorphs at nine levels along a core through the middle Pliocene Gatun Formation, Republic of Panama. CSS = carbonaceous sandstone (dark lines indicate lenses of lignite), SLT = siltstone, SS = sandstone. Each mark on the bottom scale represents 5%.

appearance of the shallow water marine dinoflagellates *Operculodinium* and *Spiniferites* (Graham, 1989a, p. 51, figs. 2–4). Diversity of palynomorphs decreases from 44% at levels 257.0–253.0', to 32% at levels 223.5–222.5' (Fig. 1), and many are represented by thick-walled fern spores (*Alsophila*, *Pteris* type 4, monolete fern spore types 1, 2) and pollen (*Ilex*) that can withstand long-distance transport, or by wind-dispersed pollen produced in large quantities that can readily be blown into depositional basins (Palmae type 1; Table 1).

The upper two levels of the Gatun core (178, 162') consist of medium-grained sandstone with dispersed organic material. Preservation of the palynomorphs is only fair, diversity is low (21%), and almost all palynomorphs are represented by thick-walled forms (fern spores, *Ilex*, Malpighiaceae) or forms belonging to anemophilous species (Palmae type 1).

Collectively, the lithology and composition of the Gatun flora reveals a dynamic landscape with fre-

quent and significant changes in the physical environment. Sedimentation began in a near-shore setting close to the source area for the palynomorphs (257.0–250.0'). The site was subsequently inundated by marine waters, reflected first by an increase in *Rhizophora* pollen (250.0'), and then by the presence of *Operculodinium* and *Spiniferites* (223.5–222.5'). The sediments and microfossil composition of the uppermost levels (178.0, 162.0') suggest uplift of the adjacent land with steeper gradients carrying coarser-grained sandstone out over the site. Lignitic lenses could not accumulate in this high-energy environment, and plant microfossils are represented by thick-walled, resistant spores and pollen (drift specimens), and by wind-dispersed pollen. Similar cycles of deposition are repeated throughout the Gatun core, and are also evident in many other Tertiary formations in this tectonically active region. The genesis of these numerous, short-term cycles was likely relatively rapid uplift and subsidence of the land, superimposed on a general eustatic rise in sea level, which



continued until about the mid-Pliocene, when levels dropped, reflecting the early stages of extensive polar glaciation (see illustration in Graham, 1987b, fig. 4). Intense tectonic activity is clearly evident in the structural geology of central Panama (Graham et al., 1985, fig. 2, p. 49, Culebra Formation; Lowrie et al., 1982, fig. 3).

The changing position of the source area vegetation relative to the Gatun core site is reflected in the diversity values noted earlier. These values (viz., percent of the total flora of 110 palynomorphs represented at each of the three groups of levels; Fig. 1) show a trend through the profile. The figures are very general, and a number of factors influence the quantitative and qualitative representation of plant microfossils in a depositional basin (e.g., distance of the basin from the source area, sediment type, rate of sedimentation, amount of sediment in each sample, number of samples for each level). Nonetheless, a decrease in diversity and an increase in thick-walled spores and pollen, and anemophilous pollen types, is evident from the bottom to the top of the Gatun core. Levels 257.0, 255.5, and 253.0' (representing 4' of sediment), with the site of deposition closest to the source area vegetation, contain 44% of the Gatun palynomorph types. Levels 223.5, 223.0, and 222.5' (representing 1' of sediment), and further removed from the source area, contain 32% of the palynomorph types. Levels 178.0 and 162.0' (16' of sediment) contain 21%, with poorer preservation and evidence of differential preservation (thick-walled pollen/spore types). Levels 257.0–253.0' are most representative of the vegetation growing in the region during Gatun time.

The 110 palynomorphs recognized for the Gatun flora are considerably more than has been recorded from the preceding early Miocene floras in southern Central America: Culebra—55 taxa; Cucaracha—21 taxa; La Boca—54 taxa; Uscari—44 taxa.

One of the principal differences between the Gatun assemblage and older Tertiary floras from the same region is the marked increase in the kinds of palynomorphs present, reflecting greater diversity in the developing southern Central American vegetation.

#### PALEOCOMMUNITIES

Some of the 110 taxa recognized from the Gatun microfossil flora indicate the presence of a specific paleocommunity (e.g., *Rhizophora*). Others are suggestive of a particular community (e.g., *Podocarpus*), especially when common associates of

that community are also present (e.g., *Alfaroa/Oreomunnea*, *Quercus*), even though these may extend into adjacent communities along transition zones, or occur as edaphically or physiographically controlled local outliers in different communities. Other taxa range widely through several community types (e.g., *Lycopodium*).

Most pollen and spore types in the Gatun assemblage can be identified only to genus, and many of the larger modern genera contain species that grow under widely different ecological conditions. For example, *Quercus oleoides* Cham. & Schldl. is a lowland tropical species, while *Q. aaata* Muller, *Q. brenesii* Trel., *Q. copeyensis* Muller, and others grow at higher altitudes in temperate habitats. Other pollen and spores can be identified only to genus or above (e.g., monolete fern spore types 1–5, Gramineae, Palmae, Ericaceae, Malpighiaceae, Melastomataceae). Unknown types 1–27 could represent taxa from any number of communities, while the pollen of some important tropical families (e.g., Lauraceae) does not preserve in the fossil record.

For these and other reasons, paleocommunity reconstructions based on palynological data alone are tentative, and provide only a general picture of the paleovegetation. The probability of some version of a modern community being represented in a fossil assemblage is enhanced, however, in descending order of importance, by the presence of (1) elements restricted to a particular community, (2) elements typical of a community, even though they may range into other vegetation types, (3) a combination of several genera that, even though individually widespread, are collectively typical of a given community, and (4) a very large number of genera that occur in a particular community even though none are restricted to, or even typical of, that particular vegetation (e.g., numerical abundance). Once a tentative model of paleocommunity types has been established, it can be assessed in terms of (1) paleophysiographic and paleoclimatic reconstructions based on other lines of evidence (e.g., paleotemperature curves, fossil vertebrate faunas), (2) plate tectonic data (viz., land–sea relationships), (3) biogeographic data on the timing and direction of migrations, and geographic affinities, derived from studies of the past (fossil occurrences) and present distribution of other taxa, (4) consistency with results from studies of other fossil floras of the same age from the same region, and (5) consistency with trends and patterns established from studies of older and younger biotas and from the above collective evidence.

Taxa identified from the Gatun flora are ar-



TABLE 2. Distribution of taxa identified from the middle Pliocene Gatun Formation among comparable community types in Panama. Placement is according to principal or most common occurrence(s), and most range through more than one community.

Shallow Water Marine Community	<i>Operculodinium</i> , <i>Spiniferites</i>
Mangrove Swamp	<i>Hibiscus</i> , <i>Rhizophora</i>
Floating/Submerged Fresh Water Aquatic Community	<i>Ceratopteris</i> , <i>Utricularia</i> , <i>Cabomba</i>
Lowland Fresh Water Marsh Community and Fringing Vegetation	Monolete fern spore types 1-2 (likely representing Blechnaceae, Polypodiaceae, Pteridaceae), Palmae type 1, <i>Bucida</i>
Tropical Wet Forest (31 taxa)	<i>Lycopodium</i> , <i>Selaginella</i> , <i>Cnemidaria</i> , <i>Ctenitis</i> , <i>Pteris</i> , <i>Aegiphila</i> , cf. <i>Aguiaria</i> , <i>Alchornea</i> , <i>Allophylus</i> , <i>Bernoullia</i> , <i>Bucida</i> , <i>Bursera</i> , <i>Chomelia</i> , <i>Combretum</i> , <i>Crudia</i> , <i>Cupania</i> , <i>Cymbopetalum</i> , <i>Erythrina</i> , <i>Eugenia/Myrcia</i> , <i>Faramea</i> , cf. <i>Glycydendrum</i> , <i>Guarea</i> , <i>Hampea/Hibiscus</i> , <i>Mortonioidendron</i> , <i>Paullinia</i> , <i>Petrea</i> , <i>Posoqueria</i> , <i>Pseudobombax</i> , cf. <i>Stillingia</i> , <i>Symplocos</i> , <i>Terminalia</i>
Tropical Moist Forest (38 taxa)	<i>Lycopodium</i> , <i>Selaginella</i> , <i>Alsophila</i> , <i>Cnemidaria</i> , <i>Cyathea</i> , <i>Ophioglossum</i> , <i>Pteris</i> , <i>Aegiphila</i> , cf. <i>Aguiaria</i> , <i>Acacia</i> , <i>Alchornea</i> , <i>Allophylus</i> , <i>Bernoullia</i> , <i>Bursera</i> , <i>Cedrela</i> , <i>Ceiba</i> , <i>Chomelia</i> , cf. <i>Cionosicyus</i> , <i>Combretum/Terminalia</i> , <i>Cosmibuena</i> , <i>Crudia</i> , <i>Cupania</i> , <i>Cymbopetalum</i> , <i>Erythrina</i> , <i>Eugenia/Myrcia</i> , <i>Faramea</i> , <i>Guarea</i> , <i>Hampea</i> , cf. <i>Jatropha</i> , <i>Mortonioidendron</i> , <i>Paullinia</i> , <i>Petrea</i> , <i>Posoqueria</i> , <i>Pseudobombax</i> , <i>Quercus</i> , <i>Serjania</i> cf. <i>Stillingia</i> , <i>Symplocos</i>
Premontane Wet Forest (27 taxa)	<i>Lycopodium</i> , <i>Selaginella</i> , <i>Alsophila</i> , <i>Cnemidaria</i> , <i>Ctenitis</i> , <i>Cyathea</i> , <i>Pteris</i> , <i>Aegiphila</i> , <i>Alchornea</i> , <i>Allophylus</i> , <i>Bernoullia</i> , <i>Cedrela</i> , <i>Combretum/Terminalia</i> , <i>Cosmibuena</i> , <i>Crudia</i> , <i>Cupania</i> , <i>Cymbopetalum</i> , <i>Erythrina</i> , <i>Eugenia/Myrcia</i> , <i>Faramea</i> , <i>Hampea</i> , <i>Petrea</i> , <i>Paullinia</i> , <i>Posoqueria</i> , <i>Serjania</i> , cf. <i>Stillingia</i> , <i>Symplocos</i>
Premontane Moist Forest (21 taxa)	<i>Ophioglossum</i> , <i>Alfaroa/Oreomunnea</i> , <i>Aegiphila</i> , <i>Allophylus</i> , <i>Bursera</i> , <i>Ceiba</i> , cf. <i>Cionosicyus</i> , <i>Combretum/Terminalia</i> , <i>Eugenia</i> , <i>Faramea</i> , <i>Hampea</i> , <i>Hauya</i> , <i>Ilex</i> , <i>Paullinia</i> , <i>Petrea</i> , <i>Posoqueria</i> , <i>Pseudobombax</i> , <i>Quercus</i> , <i>Serjania</i> , cf. <i>Stillingia</i> , <i>Symplocos</i>
Premontane Rainforest (11 taxa)	<i>Alchornea</i> , <i>Bernoullia</i> , <i>Cosmibuena</i> , <i>Cymbopetalum</i> , <i>Erythrina</i> , <i>Hampea</i> , <i>Paullinia</i> , <i>Petrea</i> , <i>Serjania</i> , cf. <i>Stillingia</i> , <i>Symplocos</i>
Lower Montane Moist Forest (12 taxa)	<i>Lycopodium</i> , <i>Selaginella</i> , <i>Alsophila</i> , <i>Cyathea</i> , <i>Grammitis</i> , <i>Ophioglossum</i> , <i>Pteris</i> , <i>Podocarpus</i> , <i>Acacia</i> , <i>Alfaroa/Oreomunnea</i> , <i>Ilex</i> , <i>Quercus</i>

TABLE 2. Continued.

Tropical Dry Forest (11 taxa)	Gramineae, <i>Acacia</i> , <i>Allophylus</i> , <i>Bursera</i> , <i>Cedrela</i> , <i>Ceiba</i> , <i>Combretum</i> , cf. <i>Jatropha</i> , <i>Posoqueria</i> , <i>Pseudobombax</i> , <i>Serjania</i>
Lower Montane Wet Forest (6 taxa)	<i>Lycopodium</i> , <i>Selaginella</i> , <i>Alsophila</i> , <i>Ctenitis</i> , <i>Cyathea</i> , <i>Pteris</i> ,
Premontane Dry Forest (6 taxa)	Gramineae, <i>Acacia</i> , <i>Bursera</i> , <i>Combretum</i> , <i>Eugenia</i> , cf. <i>Jatropha</i>
Montane Moist Forest (4 taxa)	<i>Grammitis</i> , <i>Podocarpus</i> , <i>Alfaroa</i> , <i>Quercus</i>
Montane Wet Forest (3 taxa)	<i>Cnemidaria</i> , <i>Cyathea</i> , <i>Grammitis</i>
Lower Montane Rainforest—none	
Montane Rainforest—none	

ranged into paleocommunities in Table 2, based on the occurrence of their presumed modern analogs. The Gatun Formation is primarily a shallow water marine deposit (Graham, 1991a, fig. 1), with all terrestrial pollen-bearing material coming from subsurface well cores. A shallow water marine community, and a coastal, warm-temperate to tropical depositional environment, are indicated by the dinoflagellates *Operculodinium* and *Spiniferites*. Fringing the coast was a mangrove swamp (*Rhizophora*), with the pollen form *Hampea/Hibiscus* likely representing *Hibiscus tiliaceous* L./*H. sororius* L.f., tropical beach plants. A floating/submerged fresh water aquatic community, beyond the influence of marine or brackish waters, is suggested by microfossils of *Ceratopteris*, *Cabomba*, and *Utricularia*. Also in the lowlands and not influenced by marine waters were marsh or wet-habitat communities reflected by non-tree fern spores (maximum 26%, Table 1) of the Blechnaceae, Polypodiaceae, Pteridaceae type. Some palm pollen (maximum 20%) probably represents species associated with or bordering the marsh community. *Bucida* is a small tree or shrub occurring in strand thickets and wet forests at elevations from sea level to about 1,000 m.

It is difficult to distinguish between the various lowland forest types on the basis of palynological evidence because the generic composition of these forests is often similar, and transition zones may be broad and gradual. The tropical moist forest is represented by 38 taxa that can occur in that formation, the tropical wet forest by 31 taxa, the premontane wet forest by 27 taxa, and the premontane moist forest by 21 taxa (Table 2). It is



likely that some form of all of these communities were represented in the middle Pliocene vegetation of central Panama. The premontane rainforest (11 taxa), lower montane moist forest (12 taxa), and tropical dry forest (11 taxa) are also represented by a number of taxa and/or by elements characteristic of these vegetation types. For example, the association of *Podocarpus*, *Alfaroa/Oreomunnea*, *Ilex*, and *Quercus* is most typical of the lower montane moist forest. The presence of pollen of 11 taxa that can or typically do occur in the tropical dry forest compares with the following figures from other Tertiary floras in the region:

- Gatuncillo (middle(?) to lower Eocene, Panama)—4 (+ two widespread)
- Culebra (lower Miocene, Panama)—7
- Cucaracha (lower Miocene, Panama)—0
- La Boca (lower Miocene, Panama)—0
- Uscari (lower Miocene, Costa Rica)—0

Grass pollen, virtually absent from these older floras, increases to values of 7.5%, 6.5%, and 4.5% in the Gatun flora (Table 1). Many of the Gramineae were probably associated with the tropical dry forest. One of the principal differences between the older Tertiary floras of southern Central America, and the Gatun flora, is the initial appearance of a more fully developed and widespread tropical dry forest in the middle Pliocene. In turn, this suggests that relatively extensive, sustained, and adequate food resources for moderate- to larger-sized herds of browsing and grazing mammals, migrating in substantial kinds and numbers between North and South America near the end of the Pliocene (ca. 2.4 myr), began to appear in the middle Pliocene. Prior to that time, smaller numbers of browsers and grazers were probably supported by shifting, temporal, seral communities developing in response to intense tectonic and volcanic activity, documented for southern Central America during the Tertiary (Graham, 1988b, pp. 1476–1478).

#### PALEOPHYSIOGRAPHY

Estimates of maximum altitudes in proto-Central America must be general because of the wide altitudinal range of many genera, and because montane species are underrepresented in sediments accumulating in lowland basins of deposition. However, Muller (1959) has shown that pollen from upland communities is commonly transported into coastal environments by rivers, and Germeraad et al. (1968) believe that outwashing by surface runoff is an important means of pollen transport in the tropics. This accounts, in part, for the better representation

of both entomophilous pollen types (e.g., *Cymbopetalum*, cf. *Cionosicyos*, *Acacia*, *Erythrina*, *Hampea/Hibiscus*, *Hauya*) and pollen from montane species in tropical assemblages than in temperate microfossil floras. Thick-walled spores and pollen (e.g., *Gramminitis*) and wind-dispersed types (*Podocarpus*) from inland and upland habitats are readily incorporated into coastal deposits. Thus, montane communities may be underrepresented, but not a priori absent from estuarine sediments.

The impression from the Gatun assemblage is that low to moderate montane habitats are better represented than in Eocene and lower Miocene floras from the same region. *Gramminitis*, *Podocarpus*, and *Alfaroa/Oreomunnea* are all low- to mid-elevation montane plants in southern Central America, and they occur together for the first time in the Gatun flora. Also, the number of genera that can occur in the lower montane moist forest is greater in the Gatun flora (12 genera) than in the Gatuncillo (3) or Culebra (6) floras.

Pollen assemblages from older Tertiary floras in southern Central America (Graham, 1987b, 1988c, d) indicate that all components could be accommodated within elevations ranging from sea level to about 1,400 m (Graham, 1989b). The Gatun flora suggests slightly higher elevations, to an estimated 1,700 m, within pollen rain deposition of the Gatun site. Current maximum elevations are 3,820 m (Cerro Chirripó) and 3,432 m (Volcán Irazú) in Costa Rica, and 3,475 m (Volcán Barú) in Panama, all to the west of the Gatun locality. The middle Pliocene Gatun flora provides the first evidence for low to moderate montane habitats in southern Central America.

A more extensive landscape and increased physiographic diversity accounts, in part, for the larger number of genera in the Gatun flora (110) than in other Tertiary floras from southern Central America (e.g., 55 taxa in the Culebra flora; 21 in the Cucaracha). These, in turn, sort into a greater number of paleocommunities which are better represented in the Gatun assemblage (e.g., the lower montane moist forest; tropical dry forest). In particular, the tropical dry forest may reflect the beginning of a differentiation into drier (Pacific) and wetter (Atlantic) zones in southern Central America.

#### PALEOCLIMATE

Climates of the middle Pliocene in southern Central America must have been similar to those of the present because all taxa identified from the Gatun Formation, with the exception of *Crudia*



and possibly some cf. identifications, grow in the area today. An approximation of these climates may be gained by considering those on nearby Barro Colorado Island. There the annual rainfall ranges from 190 to 360 cm (76 to 143 inches), and averages 275 cm (107.3 inches). "The climate is markedly seasonal, with a sharp dry season usually starting in mid-December and continuing until about the beginning of May. During the dry season, only 18–26 cm (7–10 inches) of rain fall" (Croat, 1978, p. 3). The development of a better defined and more extensive tropical dry forest in the middle Pliocene Gatun flora, compared to older Tertiary floras in the region, may mark the beginning of greater seasonality in the region as a consequence of increasing elevations and closure of the marine portal between North and South America.

"The atmospheric temperature may vary from as low as 16.5°C (61.7°F) to as high as 35.5°C (95.9°F), with the lowest temperatures being recorded within the forest during the rainy season and the highest at the Laboratory Clearing in the dry season. With rare exceptions the temperature ranges between 21° and 32°C (70° and 90°F) throughout the year, and the average ambient temperature in the Laboratory Clearing is 27°C (77°F). The seasonal variation in monthly averages is just 2.2°C. In the dry season the range of the monthly averages of diurnal temperature is 9–11°C, and during the rainy season it is 8–9°C. Thus the diurnal temperature variation is greater than the variation between seasons. Temperature on the forest floor is especially constant, the range of the average diurnal temperature being about 6.1°C" (Croat, 1978, p. 5).

The Tertiary microfossil floras known for northern Latin America have been placed on the global paleotemperature curve of Savin (1977; Savin & Douglas, 1985; Savin et al., 1975) by Graham (1987b, fig. 3). The middle Pliocene Gatun flora (previously considered late Miocene in age, Graham 1987b; middle Miocene, Stewart & Stewart, 1980) was deposited near the end of a temperature drop that began in the middle Miocene, and just before a slight rise in the late Pliocene that preceded the final fall toward glacial conditions in the Pleistocene. These temperature fluctuations, affecting vegetation in the north temperate region (Hubbard & Boulter, 1983; Tanai & Huzioka, 1967; Wolfe, 1978), also affected biotas as far south as 18°N latitude (viz., the Pliocene Paraje Solo flora of Veracruz, Mexico; Graham, 1976). However, at 9°N latitude the Tertiary floras of southern Central America (Uscari of Costa Rica; Gatuncillo, Culebra, Cucaracha, and La Boca of

Panama) were deposited under a different set of physiographic conditions. To the north (eastern Mexico) the setting was continental within an area of considerable physiographic relief. To the south (the Costa Rican and Panamanian Tertiary floras) the setting was insular with less physiographic relief (Dengo, 1973; Raven & Axelrod, 1974, fig. 4). As noted by Graham (1989b, c), the existence of these two physiographic provinces within northern Latin America influenced the impact of Tertiary paleotemperature changes on the terrestrial biota. In the Paraje Solo flora of Veracruz, Mexico, the impact was augmented by communities already stressed along altitudinal gradients. The Panamanian Tertiary floras were buffered against the extremes of temperature fluctuations by communities existing under lower-altitude, insular conditions in a region of considerably less physiographic diversity. Thus, the dynamics of Tertiary paleocommunities in southern Central America were driven not so much by temperature fluctuations, as with the tropical flora of southern Mexico, or by changes in sea level (and, in consequence, water tables) as with the biota of the Amazon Basin, but by changes in physiography. These changes, first evident among presently known fossil floras in southern Central America beginning in the middle Pliocene, were relatively rapid uplift and subsidence of land surfaces, increasing altitudes producing the beginnings of a rain shadow effect, and closure of the isthmian portal which affected oceanic circulation patterns that resulted in an intensification of wet and drier seasons. The biological effects were relatively rapid changes in the number, distribution, and rate of speciation of mangrove and associated lowland vegetation elements (increasing diversity of the biota), and the development of a more complex and diverse set of communities, including, especially, the lower to middle montane and tropical dry forests.

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